

Age and Growth of the Australian Freshwater Fish Murray Cod, *Maccullochella peelii peelii*

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Murray cod, *Maccullochella peelii peelii*, were sampled over the period 1975–1984 from six tributaries and two impoundments of the Murray-Darling river system in NSW; the Murray, Edward, Wakool, Murrumbidgee, Darling and Gwydir rivers, and Lake Mulwala and Lake Burrinjuck. Age determination techniques have been validated by: analysis of seasonal changes on the margins of opercular bones and whole otoliths; by close agreement between observed and back-calculated mean lengths-at-age; and by examination of known-age fish. The sharp transition from narrow, translucent zones to broad, white zones on opercular bones, and the white, opaque zones on whole otoliths have been determined to be annuli formed each spring. Opercular bones are superior for ageing cod, particularly those older than 8 years (> 800 mm).

Murray cod is a large, relatively long-lived fish; the oldest cod was estimated to be 34 years. There was no significant difference between the growth or length-weight relationships of males and females, or cod from different rivers, but cod from the impoundment, Lake Mulwala, were significantly larger than same-aged cod from rivers. The growth in length (L) of Murray cod in rivers is described by a von Bertalanffy curve, represented by the equation: $L_t = 1369.05 \{1 - \exp[-0.060(t + 5.209)]\}$. Although overall growth in length is slow (K = 0.060), there was no asymptote in the age-weight relationship for cod up to 30 years, indicating that Murray cod grow predominantly by weight increases after about 10 years of age. The length-weight relationship for cod in rivers is described by the equation: $W = 3.240 \times 10^{-9} L^{3.2592}$, where W is whole weight in kg and L is total length in mm.

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KEYWORDS: Australian percichthyid, ageing, growth rates, opercular bone, otolith, *Maccullochella*, Murray cod.

INTRODUCTION

The Murray cod, *Maccullochella peelii peelii* (Mitchell), is an Australian native, warmwater, percichthyid fish found naturally in the vast Murray-Darling river system (Fig. 1). It is Australia's largest, wholly-freshwater fish (growing to a maximum recorded size of 113.6 kg) and is highly valued by recreational and commercial fishers for its size and excellent edible qualities (Rowland 1989). There has been a dramatic decline in the abundance and a reduction in the distribution of Murray cod, particularly since the 1950s, and it is now relatively uncommon in many areas (Lake 1971; Cadwallader and Backhouse 1983; Rowland 1985, 1989).

Initial studies (Llewellyn 1966; Lake 1967; Jones 1974; Langtry, in Cadwallader 1977) used scales or otoliths to age Murray cod, but sample sizes were small, few age-classes were included, and the techniques used were not described or validated. More recently, Gooley (1992) and Anderson et al. (1992) used sectioned otoliths to age Murray cod from Lake Charlegrark (Victoria) and the Lower Murray-Darling basin. In both these studies ageing techniques were validated.

Rowland (1985) conducted a major research project into aspects of the biology of Murray cod, to provide essential data for the formulation of management policies for the

species. The age and growth component of that study is reported in this paper. Objectives were to develop reliable ageing techniques (based on opercular bone and sagittal otolith zonation) that enable accurate assessment of age in Murray cod; to compare growth rates of Murray cod from different tributaries of the Murray-Darling river system; and to determine overall growth and length-weight relationships for the species.

TABLE 1
Details of Murray cod used for age and growth analyses

River	Sampling site	No. sampled	Total length range (mm)	Weight range (kg)
Murray	Euston Weir to junction of Murrumbidgee	45	480–1270	2.1–38.1
	Lake Mulwala*	25	610–1035	4.2–36.5
Edward and Wakool	Deniliquin to Wakool	124	415–1215	1.1–34.1
Murrumbidgee	Narrandera	81	195–1220	0.07–40.0
	Lake Burrinjuck*	4	580–1095	2.9–31.0
Darling	Bourke	26	435–1080	1.2–18.6
Gwydir	Bingara	25	167–1090	0.07–22.0

* impoundment

MATERIALS AND METHODS

Murray cod were sampled from six rivers and two impoundments in the Murray-Darling river system (Table 1, Fig. 1). Between 1978 and 1984, fish were either caught by NSW Fisheries staff using drum nets, gill nets, set lines, cross-lines, droppers or angling (see Rowland 1985) or sampled from the catches of professional and recreational fishers. Each cod was measured (total length, TL) to the nearest mm, weighed (cod <10 kg to nearest 10 g, >10 kg to nearest 100 g) and sexed. In addition, data were obtained from a further 36 cod sampled by NSW Fisheries staff between 1975 and 1978.

Ageing Structures

The bony structures from each fish were stored separately in a labeled container. Different structures were examined separately and at different times, two to four weeks apart. Each bony structure was examined independently by two people, and then re-examined 6–12 months later.

Opercular bones

Opercula were removed with the aid of a scalpel and placed in hot water for two minutes. The flesh was then easily removed, the bones separated, dried and stored. Opercular bones were placed on a black background under a desk lamp and examined with the naked eye. Opercular bones from cod, TL > 800 mm were also viewed using a binocular microscope (x20) and reflected light because of the closeness of the outer annuli. There was a sharp transition or check, between distinct white and dark bands on each bone (Fig. 2). The distances from a standard point near the fulcrum to each check and to the posterior-ventral edge of the bone were measured using calipers. The nature of the margin (black or white) of each opercular bone was noted. All observations and measurements were made on the right opercular bone, unless it was damaged.



Figure 1. Localities sampled for Murray cod in the Murray-Darling river system during the period 1978 to 1984. Key to sites: 1 — Murray River; 2 — Edward and Wakool rivers; 3 — Lake Mulwala; 4 — Murrumbidgee River; 5 - Darling River; 6 — Gwydir River; star — Inland Fisheries Research Station, Narrandera.

Otoliths

Both sagittal otoliths were removed from each fish and stored dry. Otoliths were submerged, concave surface upward, in distilled water in a watchglass with a black background, and viewed using a binocular microscope and reflected light. Each otolith contained a small, distinct white focus and alternating opaque (white) and hyaline (dark) concentric zones (Fig. 3). The zones were more clearly defined on the anterior and posterior regions of the otolith. The total radius of each otolith from the focus to the medial-posterior edge, and the distance from the focus to the centre of each opaque zone along the same axis (Fig. 3) were measured using an eyepiece micrometer. The nature of the total margin, whether opaque or hyaline, was noted.

The zones were less evident in otoliths from cod, TL > 800 mm due to increased thickness of the otolith, and radii to the opaque zones were not measured in otoliths from these cod. To improve the resolution of the zones, otoliths from Murray cod, TL > 800

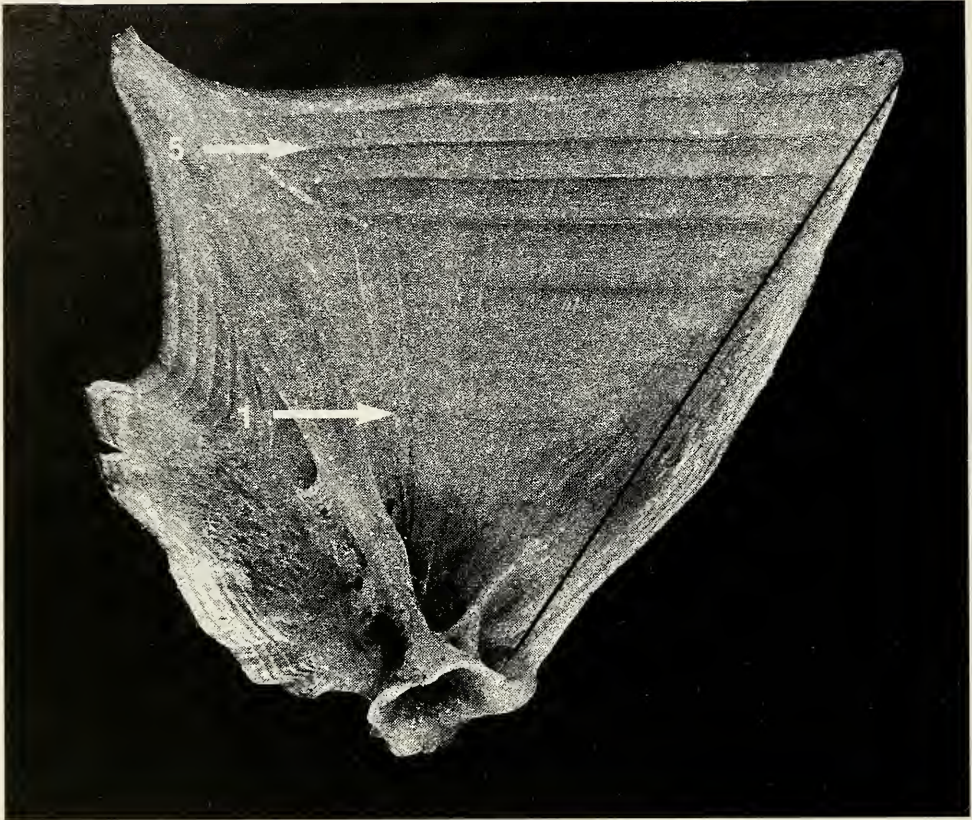


Figure 2a. Opercular bones from Murray cod used for ageing. Numbers indicate selected annuli. Distance to each annulus measured along black line. Bone (x1.5) from cod (TL 815mm, 13.3kg) sampled from Lake Mulwala in June — age 6 years, 8 months.

mm were placed in oil of clove. When the dorsal surface of the otolith was orientated towards the microscope and slightly raised, opaque and hyaline zones were distinct and could be counted along the antirostrum of the otolith.

Scales

During the initial part of the study, six non-regenerated scales were removed from midway between the anus and the closest point on the lateral line of 22 cod. The scales were cleaned in water, dried and mounted between microscope slides. The scales were examined using a binocular microscope and transmitted light.

Reference population (known-age)

Murray cod that had been artificially bred at the Inland Fisheries Research Station, Narrandera, were stocked into two 0.2-ha earthen ponds at a density of 500/ha in February 1979, and fed live food (yabbies, shrimp and goldfish) periodically. Five fish were sampled each September, November, December, February and June for the subsequent 3 years. The opercular bones, otoliths and scales of each sampled fish were examined.

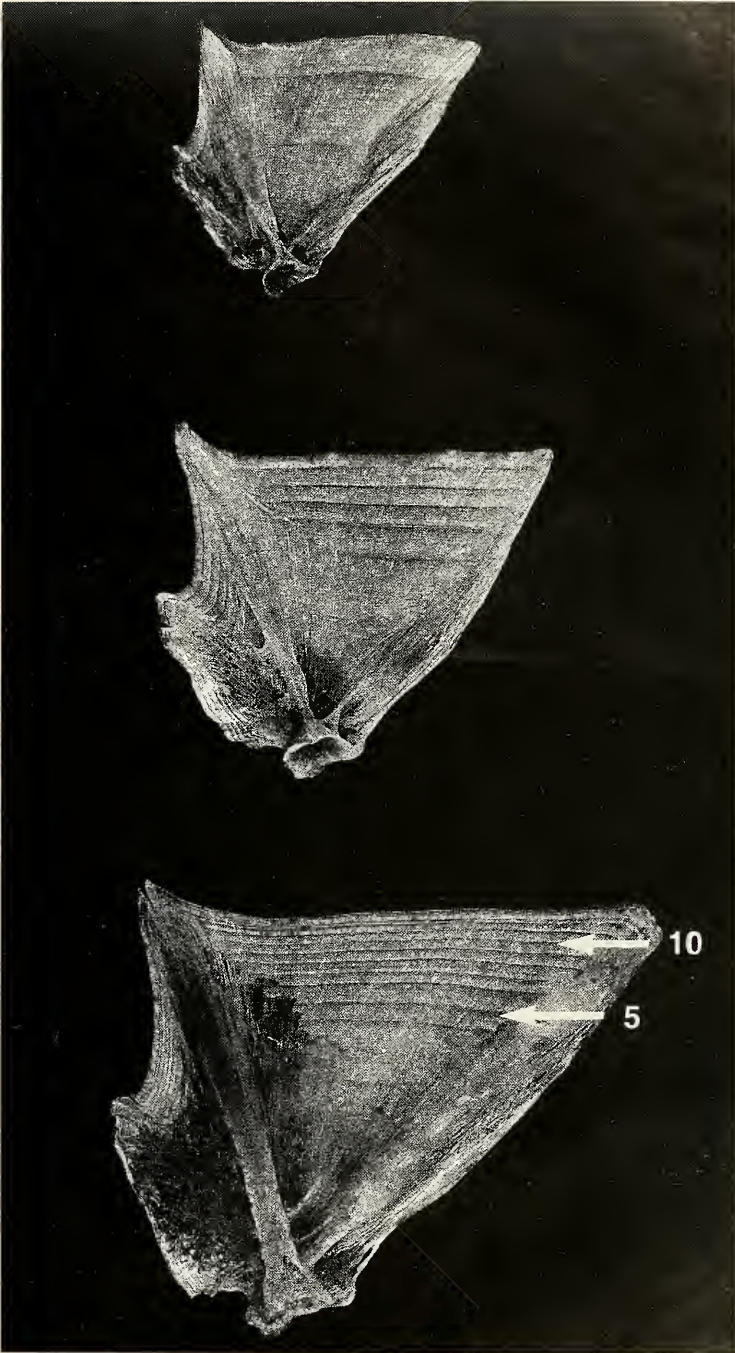


Figure 2b. Opercular bones from Murray cod used for ageing. Numbers indicate selected annuli. All bones (x0.3); top — cod (TL 580mm, 3.1kg) from the Edward River in June — age 2 years, 8 months; middle — as for (a) above; bottom — cod (TL 1085mm, 31.0kg) from Lake Burrinjuck in March — age 18 years, 5 months.

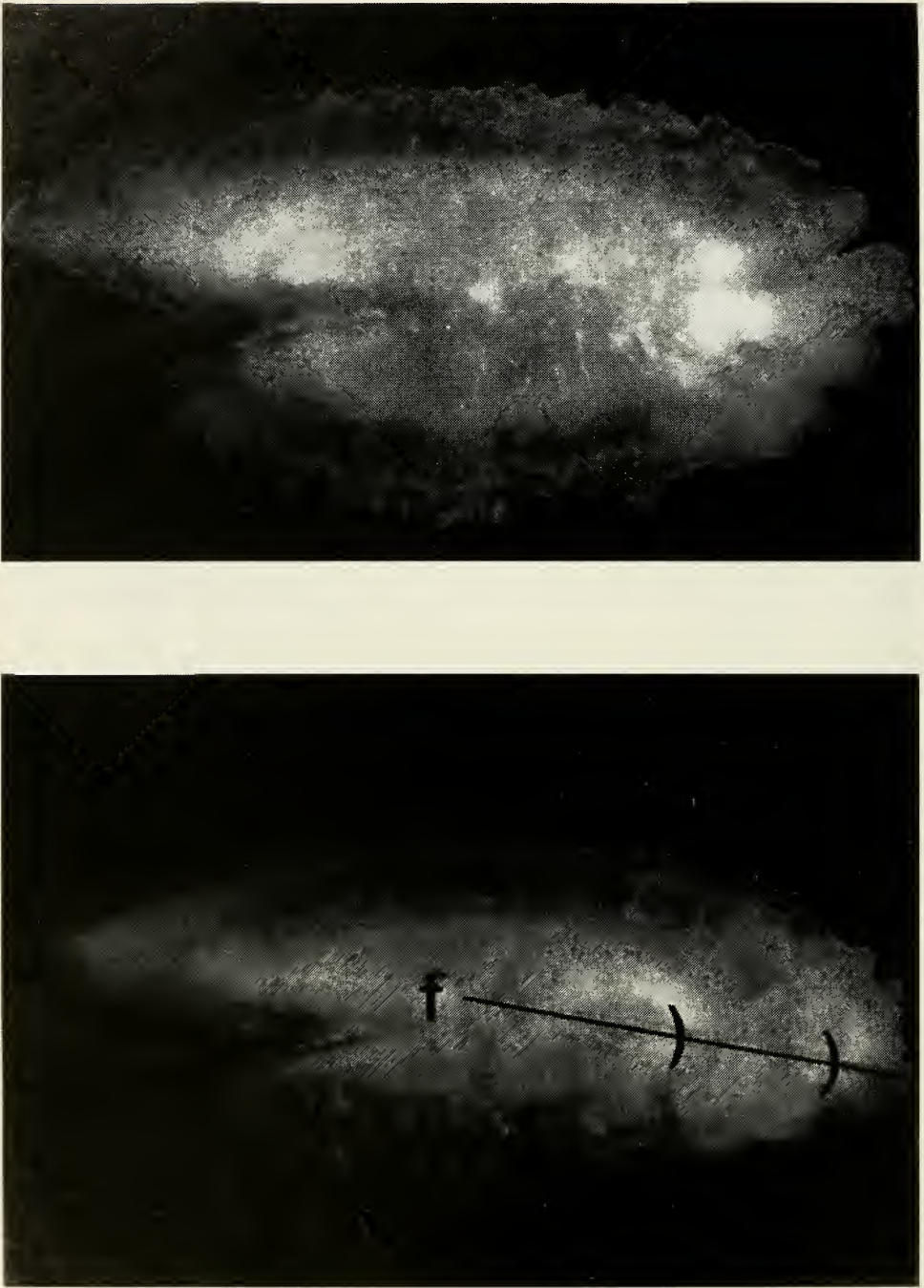


Figure 3. Sagittal otoliths ($\times 10$) from Murray cod of known age, reared in earthen ponds and sampled in February. (a) 1 year, 4 months old (TL 300mm, 0.36kg), (b) 2 years, 4 months old (TL 425mm, 1.0kg). Key to symbols: f — focus;) — centre of opaque zone.

Assigning age

Each cod was assigned an absolute age in years and months. Murray cod spawn when water temperatures rise to or above 20°C during spring (Rowland 1983, 1985, 1998) and so 1 November was defined as the birth date of cod in southern N.S.W. and 1 October for cod in the northern NSW (northern Darling and Gwydir rivers). For the calculation of mean lengths and weights at different ages, Murray cod sampled in the two months prior to an impending birth date were assigned that age. Although this is not an exact chronological age, it was considered to be biologically meaningful because it incorporates the growing and spawning seasons of each year (Barlow and Bock 1981; Rowland 1998).

Overall age and growth relationships

Comparisons between the sexes and sampling sites were conducted where sample sizes were large enough to enable statistical analyses. The mean lengths and weights of male and female cod (ages 3 to 7 years) were compared using Student's *t*-tests, and the mean lengths and weights of cod (males plus females; 3 to 7 years) from the different sampling sites were compared using one-way analysis of variance and Tukey's *w*-procedure (Steel and Torrie 1960).

The mean length-at-age data were fitted to a von Bertalanffy growth curve by non-linear least squares estimation using C.S.I.R.O. Alpha Subprogram LMM2. The growth curves for males and females were compared using the likelihood ratio test of Kimura (1980).

The relationship between fish TL and opercular bone and otolith radii were determined using regression analyses, and because the relationships were linear but not directly proportional, the following equation (from Tesch 1971) was used to estimate length-at-age by back-calculation.

$$l_n = \frac{S_n}{s} (l - c) + c$$

where l_n = length of fish when annulus "n" formed, l = length of fish when sampled, S_n = radius of annulus "n", s = total radius, and c = a constant, representing the intercept of the regression line on the Y-axis

The mean lengths of cod at ages 1 to 10 years estimated from back-calculations were compared to the observed mean lengths using Student's *t*-tests.

The length-weight relationships for fish from rivers were determined using analysis of covariance.

RESULTS

A total of 330 Murray cod (TL, range 167–1270 mm; total weight range 0.07–40.0 kg) were sampled (Table 1).

Opercular bones

Distinct transitions from dark to white margins occurred on opercular bones of known-age Murray cod between September and November during the second and third years of growth. The opercular bones of cod less than 1 year old were pale and the change in margin type in 1 year old cod was generally not apparent until February. The margins of opercular bones from 2 and 3 year cod sampled in November, December and February were generally white, and those from cod sampled in June and September were dark.

Opercular bones from 181 Murray cod (TL, 195–1270 mm; 0.08–38.1 kg) were examined. The mean monthly marginal increments on the opercular bones of 3 and 4 year old Murray cod, and the relative frequency of the different types of margins on the bones of 3 to 20 year old cod are shown in Fig. 4.

Opercular bones of Murray cod have alternating white and dark bands that are parallel to the posterior and dorsal edges of the bone (Fig. 2). The broad, white, opaque bands which are formed during the spring and summer months gradually fade into narrow, dark, translucent bands. These end abruptly with a sharp transition or check to the next white, opaque zone. The check generally occurs in October or November and the margins of opercular bones of all cod sampled in December were white (Fig. 4). The check is considered to be an annulus.

Annuli were clearly distinguishable on opercular bones from Murray cod older than 15 years of age (Fig. 2b) and with the aid of a dissecting microscope, outer annuli on the opercular bones of cod presumed to be between 20 and 34 years old could also be counted. Ossification obscured the first one or two annuli on the bones of some of these larger cod and estimation of their age depended on knowing the approximate position of the first or second annulus on opercular bones of younger cod from the sampling site.

False checks on the opercular bones of 4% of Murray cod, were identified as an abrupt, thin transparent band in the normally broad, white band deposited between spring and autumn.

Otoliths

Otoliths sampled from known-age cod less than 1 year old were slightly opaque. By November otoliths from 1 year old cod had a distinct white, opaque zone at the margin and this was surrounded by a hyaline zone in most otoliths sampled in December and in all otoliths sampled in February (Fig. 3). During the second and third years of growth, one opaque and one hyaline zone were deposited annually, and only otoliths from known-age cod sampled in November or December had opaque margins; the remainder had hyaline margins.

Otoliths from 315 Murray cod (TL, 167–1270 mm; 0.07–40 kg) were examined. The mean monthly marginal increments on the otoliths of 3 and 4 year old cod and the relative frequency of different types of margins on the otoliths of 3 to 19 year old cod are shown in Fig. 5. The mean marginal increment was highest in September and lowest in November and otoliths from 67% of cod sampled in October had opaque or narrow hyaline margins. By November the opaque zone had been formed in the otoliths of all but 6% of fish and in January all otoliths had a relatively broad hyaline margin. No false opaque or hyaline zones were identified on otoliths.

These data indicate that the opaque zone is an annulus which is deposited in the otoliths of most Murray cod during October and November.

Ages estimated using both the otoliths and opercular bones from the same fish (TL < 800 mm), were generally in agreement (93%, n=158), but the estimated ages were the same in only 50% of fish over 800 mm (n=14). Where there was disagreement, opercular bones were used to age cod TL > 800 mm. There were no obvious differences between the formation of annuli on the otoliths and opercular bones of immature and mature cod.

Scales

Distinct checks were formed annually during October and November on the scales of known-age Murray cod. Checks were also evident on the scales of cod up to 8 years of age, and the number of checks usually coincided with the age determined using opercular bones and otoliths. However, outer checks on the scales of older cod were unclear and difficult to interpret, and there was often a high proportion of regenerated scales on cod TL > 800 mm.

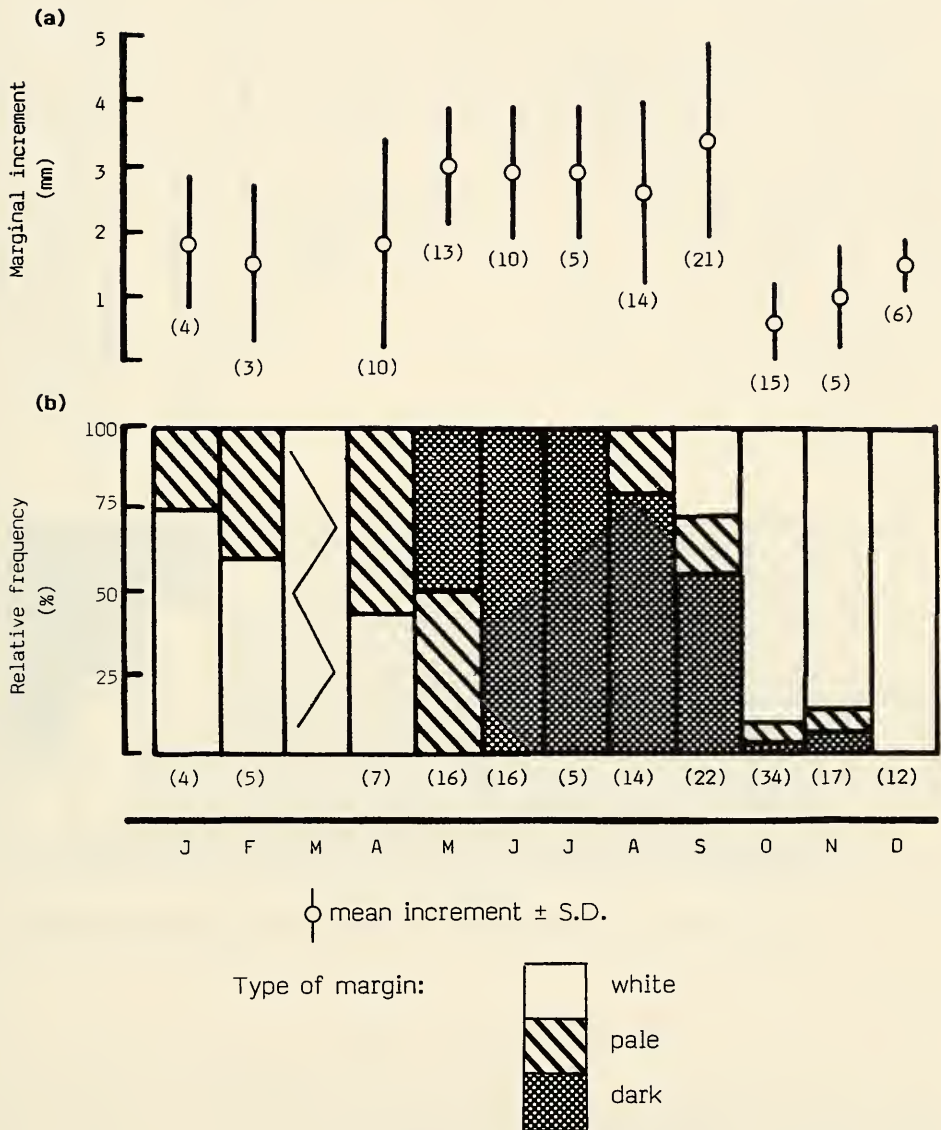


Figure 4. Size of increments and frequencies of margin types on the opercular bones of Murray cod: (a) marginal increments in 3 and 4 year old individuals; (b) relative frequency of the different types of margins in individuals from 3 to 20 years old. Opercular bones not taken from cod sampled in March. Sample sizes in parentheses.

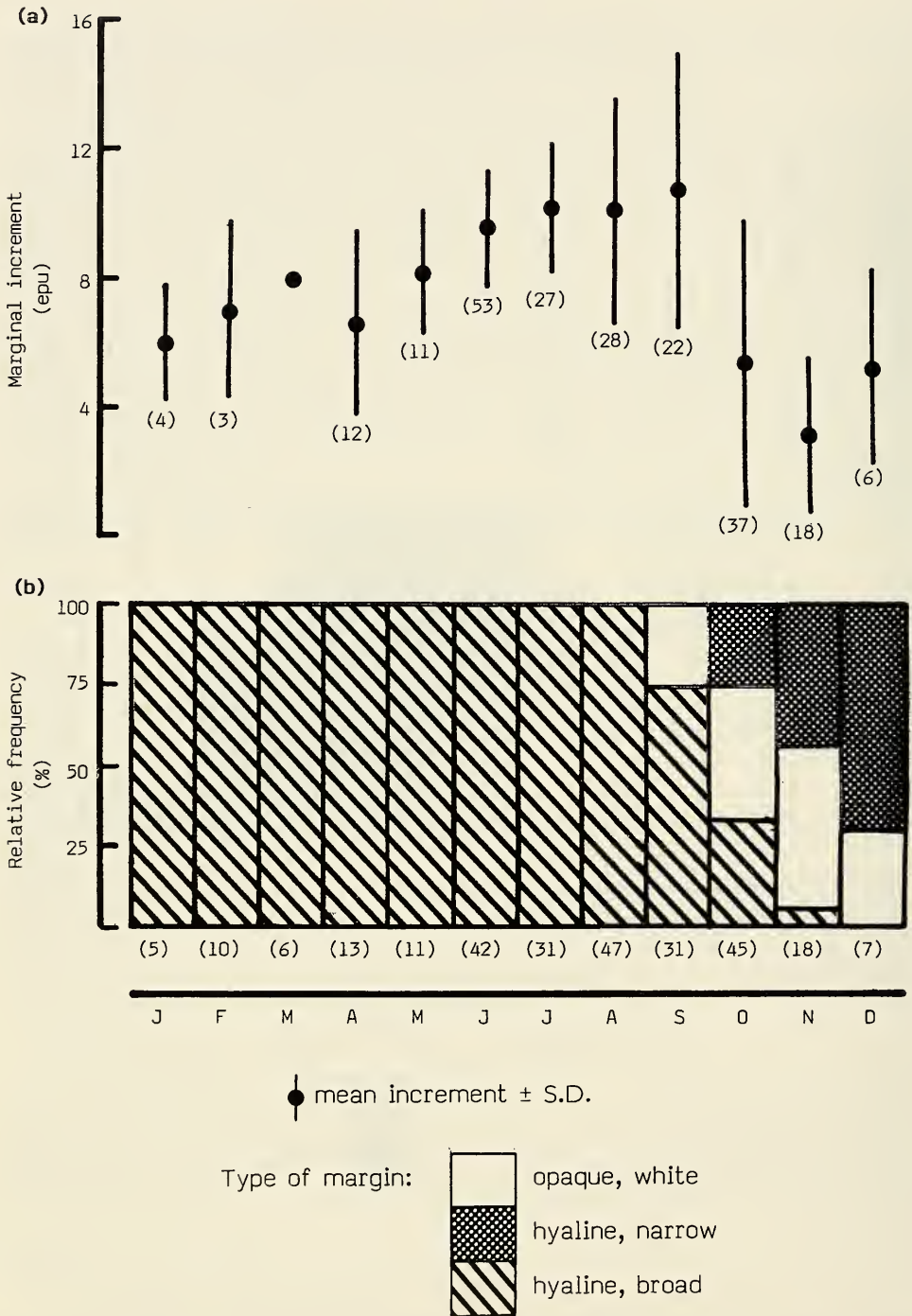


Figure 5. Size of increments and frequencies of margin types on otoliths of Murray cod: (a) marginal increments in 3 and 4 year old individuals; (b) relative frequency of different types of margin in individuals from 3 to 19 years old. Sample sizes in parentheses.

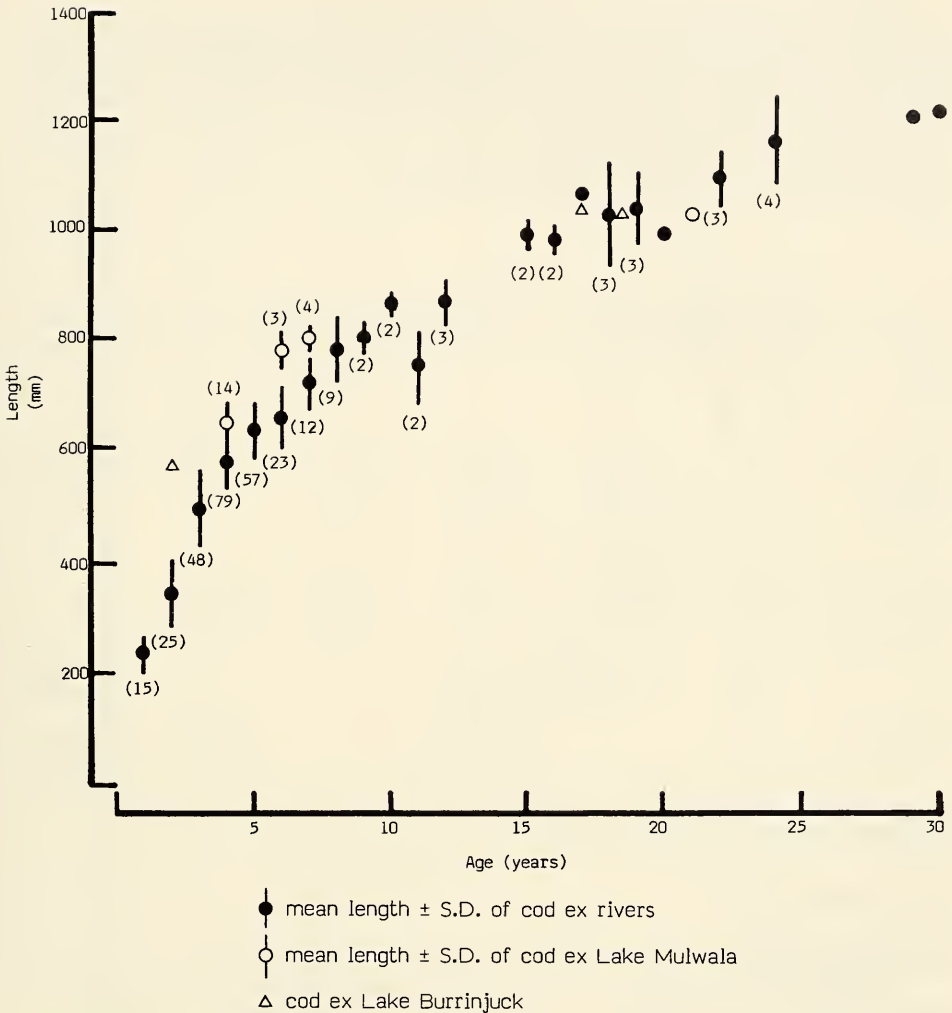


Figure 6. Total length at age in Murray cod.

Mean lengths and weights at ages

There was no significant difference ($P > 0.05$) between the mean lengths of males and females at each site with the exception of 4 year old cod from the Murrumbidgee River. Similarly, there was no significant difference ($P > 0.05$) between the mean weights of males and females at each site. Data from both sexes were pooled for further analyses. The mean lengths and weights of 3 to 7 year old Murray cod from different sites in the Murray-Darling river system are given in Table 2.

The mean weight of 5 year old Murray cod from the Murrumbidgee River was significantly ($P < 0.01$) lower than the weight of cod from other rivers (Table 2), but there was no significant difference ($P > 0.05$) in the mean lengths and weights of 3, 4, 6 and 7 year old cod from all rivers.

The 4, 6 and 7 year old Murray cod from Lake Mulwala were significantly longer ($P < 0.05$) than same-age cod from one or more of the other sampling sites, and cod from the lake were significantly heavier ($P < 0.01$) than same-aged cod from all other sampling sites (Table 2). The four Murray cod sampled from Lake Burrinjuck were also heavier than same-age cod from rivers (Fig. 7).

The mean lengths and the mean weights of 1 to 30 year old Murray cod from all sampling sites are shown in Figs. 6 and 7 respectively.

TABLE 2

Length (L) (mm) and weight (W) (kg) of 3 to 7 year old Murray cod from different rivers and Lake Mulwala. Data are means \pm s.d., with sample sizes in parentheses.

Rivers		Age (years)				
		3	4	5	6	7
Murray,	L	503 \pm 57(20)	584 \pm 50(47)	652 \pm 48(42)	662 \pm 53(18)	695 \pm 39(5)
Edward, Wakool	W	2.0 \pm 0.7(19)	3.5 \pm 1.0(47)	5.0 \pm 1.2(42)	5.4 \pm 1.5(20)	6.7 \pm 1.8(5)
M'bidgee	L	470 \pm 88(16)	560 \pm 33(14)	581 \pm 50(7)	—	746 \pm 27(5)
	W	1.8 \pm 1.1(18)	2.9 \pm 0.5(16)	3.1 \pm 1.0(10)*	—	6.8 \pm 1.2(4)
Darling	L	502 \pm 96(2)	568 \pm 36(11)	636 \pm 26(6)	651 \pm 37(5)	—
	W	2.3 \pm 1.5(2)	3.5 \pm 0.9(11)	4.3 \pm 0.6(6)	6.0 \pm 1.7(6)	—
Gwydir	L	537 \pm 36(10)	599 \pm 39(7)	583 \pm 74(2)	—	769 \pm 55(2)
	W	2.2 \pm 0.5(10)	3.6 \pm 0.2(6)	—	—	7.6 \pm 2.1(2)
Lake Mulwala	L	—	654 \pm 35(14)#	—	786 \pm 32(3)#	806 \pm 8(4)#
	W	—	5.8 \pm 0.8(14)*	—	9.6 \pm 1.5(3)*	10.9 \pm 1.8(4)*

* significantly different ($P < 0.01$) within age class.

significantly different ($P < 0.05$) within age class.

Growth relationships

von Bertalanffy growth curve

The growth curves for 1 to 30 year old male and female Murray cod from rivers are represented by the equations:

$$L_t (\text{male}) = 1367.61 \{1 - \exp[-0.059(t + 5.604)]\}$$

$$L_t (\text{female}) = 1371.84 \{1 - \exp[-0.061(t + 4.868)]\}$$

There was no significant difference between these growth curves ($X^2 [-N \ln (r^2)] = 0.3398$, d.f. = 3, $P > 0.01$), and the growth curve (Fig. 6) of Murray cod from rivers in the Murray-Darling river system is represented by the equation:

$$L_t = 1369.05 \{1 - \exp[-0.060(t + 5.2090)]\}$$

Back-calculation of age

The mean lengths of 1 to 10 year old Murray cod, both observed and those determined by back-calculation are given in Table 3. Mean lengths at ages 1 and 2 were significantly ($P < 0.01$) larger than observed mean lengths; however, mean lengths at most other ages were in agreement.

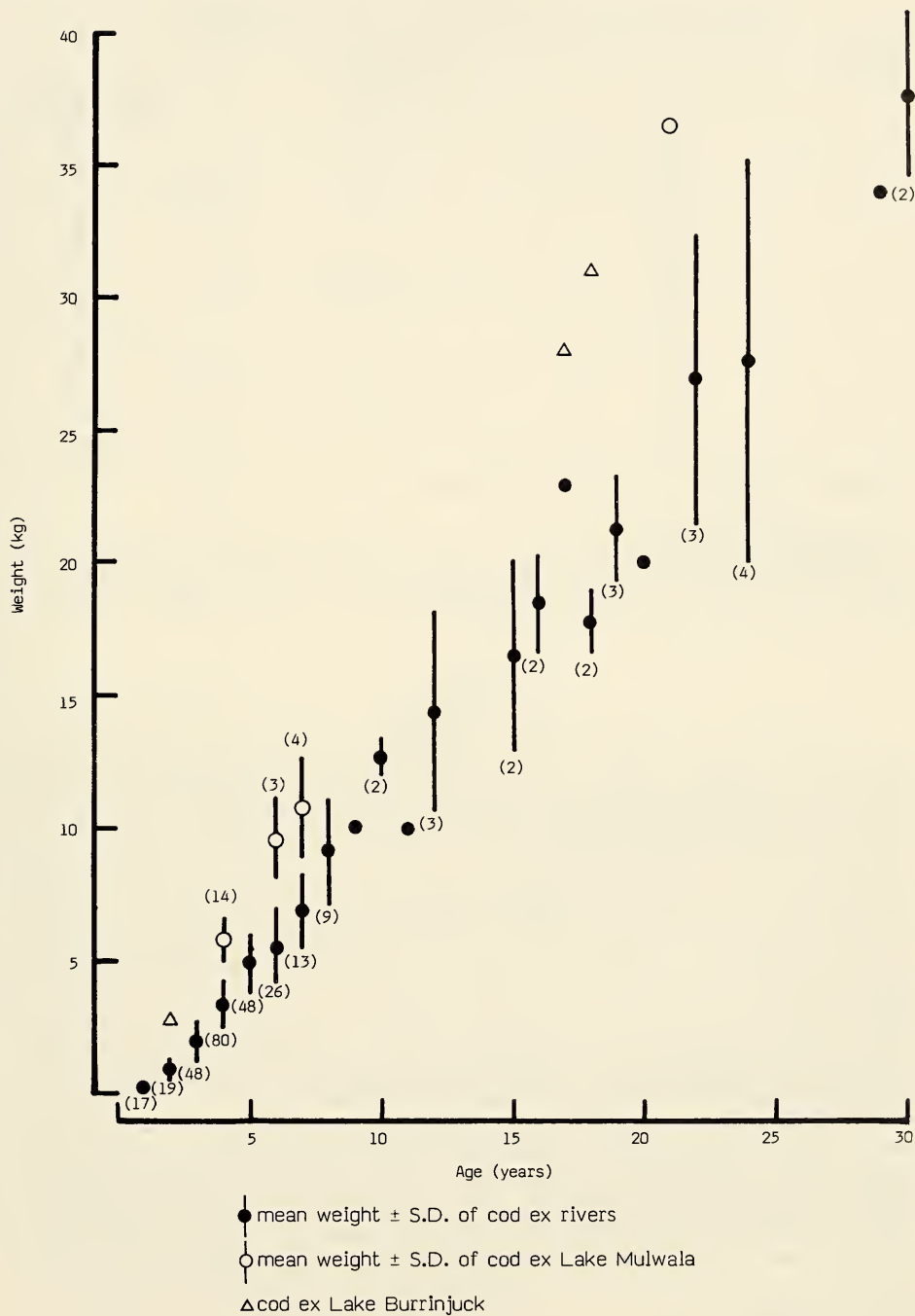


Figure 7. Weight at age in Murray cod.

TABLE 3
Observed and back-calculated mean lengths of 1 to 10 year old Murray cod.

Age (years)	Length (mm)		
	Observed	Back-calculated; otoliths	Back-calculated; opercular bones
1	236	322*	279*
2	348	429*	404*
3	499	519	512
4	579	592	580
5	639	638	613
6	663	704*	683
7	728	748	723
8	787	784	767
9	803	830	800
10	869	827	824

* significantly different ($P < 0.01$) from observed mean length.

Length-weight relationships

The length-weight relationships of Murray cod from rivers and Lake Mulwala are: rivers $W = 3.240 \times 10^{-9}L^{3.2592}$ (Fig. 8); Lake Mulwala $W = 3.684 \times 10^{-9}L^{3.2592}$, where W is whole weight in kg and L is total length in mm.

DISCUSSION

Validation of techniques is an essential part of fish age and growth studies (Beamish and McFarlane 1983). The techniques for ageing Murray cod were validated by examination of the seasonal changes on the margins of opercular bones and otoliths from known-age and wild-caught fish, and by the close agreement between the observed and back-calculated mean lengths-at-age. It is possible that the differences between the observed and back-calculated mean lengths at ages 1 and 2 were due to inaccuracies in measuring the radii, or selective sampling and differential growth rates of 1 and 2 year old cod between rivers. There may also be differential growth rates of larval and juvenile cod between rivers. In 1979, the Murray, Edward and Wakool rivers, but not the Murrumbidgee River, were at or near flood level (Rowland 1998) and it was from the former rivers that many cod from a strong 1979 year class were sampled in 1983 as 4 year old fish for the age and growth analysis (Table 1). The significantly greater back-calculated mean lengths at ages 1 and 2, may reflect rapid growth of larval and juvenile cod in the Edward and Wakool rivers during the 1979 flood.

Checks are formed on both the opercular bones and otoliths of most juvenile and adult Murray cod annually during October and November, and because Murray cod breeds during these months (Rowland 1983, 1998; Cadwallader and Gooley 1985) cod can be directly aged by counting checks. There was no evidence of the subsidiary growth rings on the bony structures in Murray cod as mentioned by Llewellyn (1966), and no otoliths and only 4% of the opercular bones examined had apparent false checks.

Ageing structures

Le Cren (1947) used opercular bones to age perch, *Perca fluviatilis*, and he also found that the sharp transition from the narrow, transparent winter band to the broad,

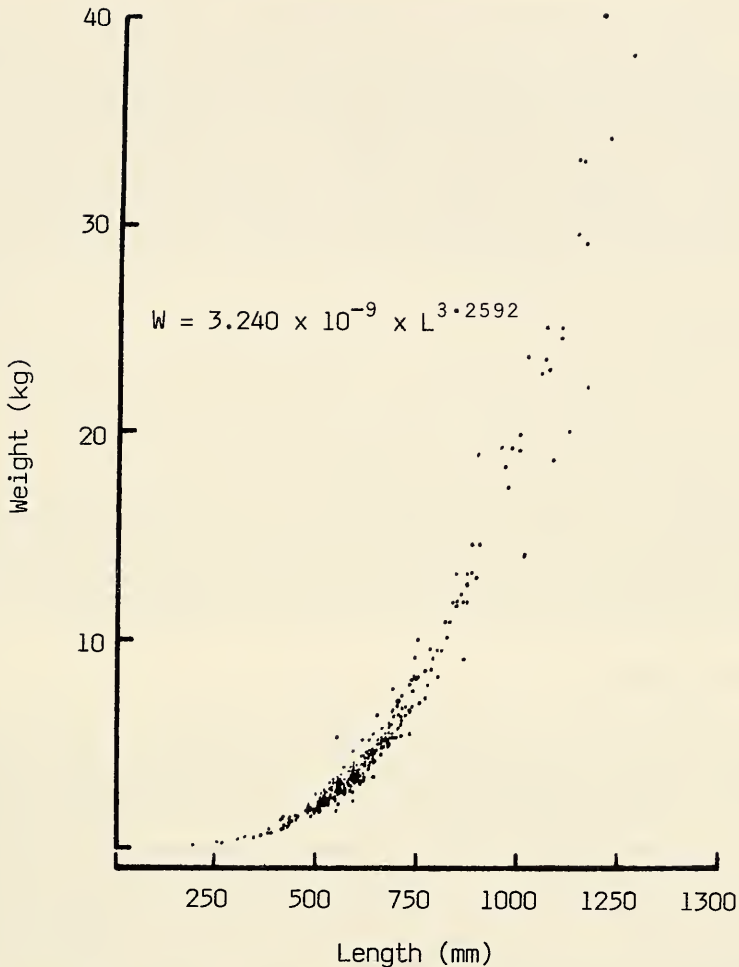


Figure 8. Relationship of total length to weight of Murray cod (both sexes) from the Murray, Edward, Wakool, Murrumbidgee and Darling rivers (n = 292).

opaque summer band was an annulus in that species. Although opercular bones are not commonly used to age fish, McConnell (1951) and Mann (1973) found opercular bones superior to other bony structures for age determination, particularly for older year-classes. Scopetstone (1988) used opercula to age the cui-ui, *Chasmistes cujus*, up to 41 years, and to demonstrate that some species of catostomids and cyprinids of western North America were older than had previously been thought. In the current study, checks could be counted on the opercular bones of Murray cod estimated to be 29, 30 and 34 years old. The use of opercular bones in these studies demonstrate that these bones are valuable in age and growth studies of long-lived fishes.

The otoliths of most fish in temperate regions consist of alternating broad, opaque zones which are formed during periods of rapid growth, generally in spring and summer, and narrow, hyaline zones formed during periods of slow growth (Jearld 1983). Previous authors have identified the hyaline zone (Jensen 1970; Dark 1975), the opaque zone

(Watson 1964; Manooch and Haimovici 1978; Johnson et al. 1983) or the distal or proximal edges of either zone (Sikstrom 1983; Moore and Labisky 1984) as annuli on the otoliths of different species of fish. In Murray cod the annulus was the opaque zone which commenced to form in otoliths in late September or early October and was generally completed by December and surrounded by part of the following hyaline zone in January. This pattern was also reported in broken and sectioned Murray cod otoliths by Gooley (1992) and Anderson et al. (1992). The increasing thickness and opaqueness of otoliths in large cod made the use of this bony structure difficult and unreliable; however, Anderson et al. (1992) were able to age cod up to 48 years (1400 mm and 47.3kg) using sectioned otoliths.

Age comparisons

Murray cod is a relatively long-lived Australian freshwater fish; the oldest cod in the current study was estimated to be 34 years. The maximum ages of cod in the studies by Anderson et al. (1992) and Gooley (1992) were 48 and 22 years respectively. These studies demonstrate that Murray cod is the longest lived percichthyid and possibly freshwater fish in Australia. The maximum reported ages of two other native percichthyid fishes are 22+ in the Australian bass, *Macquaria novemaculeata* (Harris 1985) and 19+ years in the golden perch, *Macquaria ambigua* (Battaglene 1991). These data greatly exceed the maximum age of 14 years reported by Davis (1984) for another large, Australian freshwater fish the barramundi, *Lates calcarifer* (Centropomidae).

Growth and variability

An L value for Murray cod of 1369 mm is close to 1270 mm, the maximum length observed, indicating that a von Bertalanffy growth curve adequately describes the growth of Murray cod sampled during this study. The value is also similar to that ($L = 1202$ mm) determined by Anderson et al. (1992). However, Whitley (1955) stated that cod grow to 1800 mm, and the 113.6 kg cod caught in the Barwon River in 1902 (Rowland 1989) would have been approximately 1750 mm according to the length-weight relationship determined in the current study. It is apparent that Murray cod can far exceed the observed and theoretical maximum sizes reported in this paper. The calculation of L depends on the number of age groups and individuals used, and a higher value of L would probably have been obtained if more cod longer than 1000 mm could have been aged and included in the calculations.

The growth rate (in length) of Murray cod is slow ($K = 0.060$). Long-lived fishes generally have low K values. Populations of the snowy grouper, *Epinephelus niveatus*, a fish which may attain ages of greater than 30 years, have growth coefficients of 0.063 to 0.087 (Moore and Labisky 1984). By contrast, the growth coefficient of the relatively short-lived (8 years) Australian freshwater catfish, *Tandanus tandanus*, from the Gwydir River is 0.341 (Davis 1977). It has been suggested that in marine, reef fishes the rate of attainment of maximum size reflects the trophic level and that fishes at high trophic levels have low K values compared to fish which feed at lower trophic levels (Grimes 1978; Johnson 1983). If this hypothesis also applies to fishes in freshwater habitats, the low K value of Murray cod which is the largest carnivore in the Murray-Darling river system, would be expected.

The high value of the constant b (3.2592) in the equation describing the length-weight relationship, indicates that Murray cod become more and more rotund as their length increases. This is supported by Gooley (1992) who calculated an identical value for b. Length and weight-at-age data and the length-weight relationship indicate that, after about 10 years of age, cod grow predominantly by increases in weight. From ages 10 to 30 years, there are large variations between the weights of same-aged fish and there

is no asymptote apparent in the age-weight relationship of Murray cod up to 30 years of age (Fig. 7).

Murray cod from Lake Mulwala were significantly larger than same-aged cod from the rivers. Temperature is a major factor affecting the growth rate of Murray cod in farm dams (Barlow and Bock 1981) and feeding activity and therefore the growth rate of Murray cod in most Victorian waters is reduced by low water temperatures during winter (Cadwallader and Backhouse 1983). Water temperatures are generally lower in Lake Mulwala than in more western parts of the system. Lake Mulwala is upstream of the sampling sites in the Murray, Edward and Wakool rivers, and effects of the coldwater discharge from the base of Hume Weir extend to the lake (Walker 1980). The rapid growth rate of Murray cod in the relatively cool Lake Mulwala suggests that other environmental factors such as habitat type, food type and availability, and/or population size may play major roles in determining growth rate in Murray cod.

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REFERENCES

- Anderson, J.R., Morison, A.K. and Ray, D.J. (1992). Age and growth of Murray cod, *Maccullochella peelii* (Perciformes : Percichthyidae), in the Lower Murray-Darling Basin, Australia, from thin-sectioned otoliths. *Australian Journal of Marine and Freshwater Research* **43**, 983–1013.
- Barlow, C.G. and Bock, K. (1981). 'Fish in Farm Dams'. (N.S.W. State Fisheries, Sydney).
- Battaglene, S.C. (1991). The golden perch, *Macquaria ambigua* (Pisces : Percichthyidae) of Lake Keepit, NSW. M.Sc. Thesis, University of NSW, Sydney.
- Beamish, R.J. and McFarlane, G.A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **112**, 735–743.
- Cadwallader, P.L. (1977). J.O. Langtry's 1949–50 Murray River investigations. *Fisheries and Wildlife Paper, Victoria* (13), 1–70.
- Cadwallader, P.L. and Backhouse G.N. (1983). 'A Guide to the Freshwater Fish of Victoria'. (Government Printer, Melbourne).
- Cadwallader, P.L. and Gooley, G.J. (1985). 'Propagation and Rearing of Murray Cod *Maccullochella peelii* at the Warmwater Fisheries Station Pilot Project Lake Charlegrark'. (Government Printer, Melbourne).
- Dark, T.A. (1975). Age and growth of Pacific hake, *Merluccius productus*. *Fisheries Bulletin* **73**(2), 336–355.
- Davis, T.L.O. (1977). Age determination and growth of the freshwater catfish, *Tandanus tandanus* Mitchell, in the Gwydir River, Australia. *Australian Journal of Marine and Freshwater Research* **28**, 119–137.
- Davis, T.L.O. (1984). Age and growth studies on barramundi, *Lates calcarifer* (Bloch), in Northern Australia. *Australian Journal of Marine and Freshwater Research* **35**, 673–689.
- Gooley, G.J. (1992). Validation of the use of otoliths to determine the age and growth of Murray cod, *Maccullochella peelii* (Mitchell) (Percichthyidae), in Lake Charlegrark, Western Victoria. *Australian Journal of Marine and Freshwater Research* **43**, 1091–1102.
- Grimes, C.B. (1978). Age, growth and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina waters. *Transactions of the American Fisheries Society* **107**, 454–456.
- Harris, J.H. (1985). Age of Australian bass, *Macquaria novemaculeata* (Perciformes: Percichthyidae), in the Sydney Basin. *Australian Journal of Marine and Freshwater Research* **35**, 427–440.
- Jearld, A. (1983). Age determination. In 'Fisheries Techniques' (Eds. L.A. Nielsen and D.L. Johnson), pp. 301–324. (American Fisheries Society, Bethesda).
- Jensen, A.C. (1970). Validation of ages determined from otoliths of gulf of Maine cod. *Transactions of American Fisheries Society* **99**(2), 359–362.
- Johnson, A.G. (1983). Age and growth of yellowtail snapper from South Florida. *Transactions of American Fisheries Society* **112**, 173–177.

- Johnson, A.G., Fable, W.A., Williams, M.L. and Barger, L.E. (1983). Age, growth and mortality of king mackerel, *Scomberomorus cavalla*, from the South-eastern United States. *Fisheries Bulletin* **81**(1), 97–106.
- Jones, W. (1974). Age determination and growth studies of four species of fish from the River Murray". B.Sc.(Hons) Thesis, University of Adelaide.
- Kimura, D.K. (1980). Likelihood methods for the von Bertalanffy growth curve. *Fisheries Bulletin* **77**, 765–776.
- Lake, J.S. (1967). Freshwater fish of the Murray-Darling river system. *N.S.W. State Fisheries Research Bulletin* (7), 1–48.
- Lake, J.S. (1971). 'Freshwater Fishes and Rivers of Australia'. (Thomas Nelson, Sydney).
- Le Cren, E.D. (1947). The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. *Journal of Animal Ecology* **16**(2), 188–204.
- Llewellyn, L.C. (1966). Age determination of native inland fish of N.S.W. *The Fishermen* **2**(4), 14–19.
- Mann, R.H.K. (1973). Observations on the age, growth, reproduction and food of the roach *Rutilus rutilus* (L.) in two rivers in southern England. *Journal of Fish Biology* **5**, 707–736.
- Manooch, C.S. and Haimovici, M. (1978). Age and growth of the gage, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the south eastern United States. *Transactions of the American Fisheries Society* **107**(2), 234–240.
- McConnell, W.J. (1951). The opercular bone as an indicator of age and growth of the carp, *Cyprinus carpio* Linnaeus. *Transactions of the American Fisheries Society* **81**, 138–149.
- Moore, C.M. & Labisky, R.F. (1984). Population parameters of a relatively unexploited stock of snowy grouper in the lower Florida Keys. *Transactions of the American Fisheries Society* **113**, 322–329.
- Rowland, S.J. (1983). Spawning of the Australian freshwater fish Murray cod, *Maccullochella peelii peelii* (Mitchell), in earthen ponds. *Journal of Fish Biology* **23**, 525–534.
- Rowland, S.J. (1985). Aspects of the biology and artificial breeding of the Murray cod, *Maccullochella peelii peelii*, and the eastern freshwater cod, *M. ikei* sp. nov. (Pisces: Percichthyidae). Ph.D. Thesis, Macquarie University, Sydney.
- Rowland, S.J. (1989). Aspects of the history and fishery of the Murray cod, *Maccullochella peelii peelii* (Mitchell) (Percichthyidae). *Proceedings of the Linnean Society N.S.W.* **111**, 201–213.
- Rowland, S.J. (1998). Aspects of the reproductive biology of the Murray cod, *Maccullochella peelii peelii*. This volume.
- Scopetone, G.G. (1988). Growth and longevity of the Cui-ui and longevity of other catostomids and cyprinids in western North America. *Transactions of the American Fisheries Society* **117**, 301–307.
- Sikstrom, C.B. (1983). Otoliths, pectoral fin ray and scale age determinations for Arctic grayling. *Progressive Fish Culturist* **45**(4), 220–223.
- Steel, R.G.D. & Torrie, J.H. (1960). 'Principles and Procedures in Statistics'. (McGraw-Hill, New York).
- Tesch, F.W. (1971). Age and growth. In 'Methods of Assessment of Fish Production in Freshwater'. (Ed. W.E. Ricker), pp. 98–130. (Blackwell, Oxford).
- Walker, K.F. (1980). The downstream influence of Lake Hume on the River Murray. In 'An Ecological Basis for Water Resource Management'. (Ed. W.D. Williams), pp. 182–191. (Australian National University Press, Canberra).
- Watson, J.E. (1964). Determining the age of the young herring from the otoliths. *Transactions of the American Fisheries Society* **93**(1), 11–20.
- Whitley, G.P. (1955). The largest (and the smallest) Australasian fishes. *Australian Museum Magazine* **XI**(10), 329–332.